RECENT STUDIES OF PHAEOPHYCEAE AND THEIR BEARING ON CLASSIFICATION

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Introduction

During the past decade there has been so fundamental an advance in our knowledge of the reproductive processes and life history of the Phaeophyceae, that it seems to exceed in importance the change in viewpoint regarding any other group of plants during the same period. The work which must so largely overturn our ideas has mainly been done by European algologists, and has not been followed up in this country by any confirmatory studies; indeed, it seems to be little known. As each succeeding paper, and several from independent sources have now appeared, confirms the critical points of the others, it seems desirable at this time to review the situation and to indicate the necessary changes in the classification of the group. To date the only review in English of the studies in question is a short one by LEWIS (11), written at an early stage. Three have appeared in France, one by CONSTANTIN (1), and two by PECHOUTRE (16, 17), these latter of special value.

Historical

The pioneer in this field, to whom falls the honor of making the first clear advance, is SAUVAGEAU. Previous to the appearance of the standard texts, he, with other workers, had cleared up the normal life history of *Cutleria*, showing the relation of *Aglaozonia* as the sporophyte stage, and showing the variations in the life history (parthenogenesis, etc.) which appeared under various conditions (18, 19, 22, 23, 24). Further, his studies on members of the Sphacelariaceae and Ectocarpaceae have done much to help in the understanding of those families (20, 21, 33). Most important in the present connection, however, are his results from cultures of Laminariaceae (25–30, 32). In 1910 DREW (2) described the products of the unilocular sporangia on the surface of the *Laminaria* frond as functioning as gametes, and as producing a somewhat filamentous stage from which the mature *Laminaria* was vegetatively developed. A paper by KILLIAN (5) the following year, in discussing the development and structure of *Laminaria*, agreed, so far as it went, with the statements of DREW. This decidedly unexpected phenomenon of the sexual fusion of what from their origin should be zoospores met with considerable doubt, however, and was attacked by WILLIAMS (37), who claimed that it was not the motile zoospores of *Laminaria*, but other organisms, which had been seen to fuse by DREW. The first of SAUVAGEAU's papers on the life history of the Laminariaceae appeared as a series on *Saccorhiza bulbosa* (25, 26, 27). Here he showed that in the case of the female the germinating zoospores from the unilocular sporangia produce a one to few-celled filament. The cells of this filament enlarge and emit a non-motile egg, which seemed to be fertilized *in situ* at the aperture, where it developed into a young sporophyte. The male plant is more complex, of five or six cells and slightly branched, with several more or less clustered antheridia. Germination of the zoospores within the sorus in which they were formed was seen, and it was found that the sporelings were both male and female, demonstrating that the sporangia on one plant produced both sorts.

Following this study appeared one on two species of *Laminaria*, *L. flexicaulis* (*L. digitata*) and *L. saccharina* (28, 30). SAUVAGEAU found that in germination the chromatophore of the spore divides (the zoospore on attaching itself rounds up and forms a firm wall), and one half passes into the germ tube as it elongates. The nucleus also divides, and one daughter nucleus with a chromatophore passes toward the inflated distal end of the tube, where it is cut off by a transverse wall. The nucleus which remains behind disorganizes more or less rapidly, while the cell with the other nucleus develops the gametophyte. Some of the male filaments are short, but others are elongate and markedly branched, forming the antheridia laterally on the branches toward the end. One sperm is formed in each antheridium, and the sperms are shed before the female gametophytes in the same culture reach maturity. The female gametophytes are from one to several cells in extent, all cells being able to form eggs. Each cell swells, elongates, and the egg emerges through a terminal rupture at the end of the protuberance. The opening of the oogonium forms a sheath around the base of the egg, which develops into the young sporophyte while attached to the gametophyte. Actual fusion of the gametes was not observed.

Promptly following the papers on *Laminaria*, SAUVAGEAU published a similar study of *Alaria esculenta*, belonging to a different section of the same family. The gametophytes differed from the previous cases in several particulars. The "embryo spore," or zoospore, which has passed into the resting stage, persists and may give rise to a second filament opposite the first. The gametophytes are also larger, and the female has elongate cells, part of which only seem to produce eggs. The fertile cells form irregular lobes instead of remaining of the usual simple ovoid form, but only one egg is extruded from each cell. Sometimes the female thallus is reduced to a single cell, as is not infrequent in *Laminaria*, but is more often of from two to four cells, with the terminal one becoming fertile first, and then occasionally some of the others.

In the same year that the *Laminaria* and *Alaria* studies of SAUVAGEAU were announced (1916), KYLIN published a paper on an independent study of the life cycle of *Laminaria digitata* which confirmed the statements of SAUVAGEAU in all essential respects (8). KUCKUCK (7) and PASCHER (15) also later published confirmatory accounts of studies on *Laminaria saccharina*. The latter describes a most interesting departure, where he found that occasionally cells of the very young sporophyte, or even the undivided egg, might function as unilocular sporangia producing 2, 4, 8, or 16 zoospores. Finally, IKARI (4) described the gametophytes of *Laminaria religiosa*, which are like the two species already studied in most points, but at times have the antheridia in rows at the ends of the branches of the thallus, and shed the sperm by a terminal pore.

In the year following his papers on *Laminaria*, SAUVAGEAU gave an account of the development of *Dictyosiphon foeniculaceus*, which demonstrated another unsuspected type of alternation. The evident plant of *Dictyosiphon* only produces unilocular sporangia.

SAUVAGEAU succeeded in getting good cultures in which the zoospores germinated quickly to form a branched filamentous thallus of considerable extent, reaching a millimeter in diameter and forming hairs. When mature, cylindrical gametangia are formed with two to twelve loculi. Each cell forms a single gamete. The septae disappear before dehiscence, and the isogamous gametes escape by a terminal pore. Conjugation was not observed, but was undoubtedly present, for a part of the rounded up, quiescent cells produced from the gametes had two nuclei and two chromatophores. Germination soon took place, and produced a short filament which in a few weeks gave rise to an erect thallus with the essential structure of *Dictyosiphon*.

It is a matter of peculiar satisfaction that the work of KYLIN (10) definitely shows *Chorda* to have the same sort of life history as *Laminaria*. The vegetative similarities which this genus shows to the kelps are not sufficient alone to place it in the same family, but the demonstration of a precisely similar life cycle removes all question of the relationship. The gametophytes are considerably larger than those of *Laminaria*. KYLIN was able to confirm the cultural studies by some incomplete cytological details. In the vegetative cells of the sporophyte tissue there are present forty chromosomes. Reduction divisions take place in spore formation, and are followed by two vegetative haploid divisions. Good fixation was prevented by the paraphyses, and countable metaphases were not found, but synapsis, diakinesis, and other conditions typical of the first reduction division were recognized. The number of chromosomes was about twenty, although it could not be determined precisely. In addition to the study of the preceding species, KYLIN has given details of at least part of the life cycle of several other genera in other families, which will be discussed in connection with the changes in the classification of those families.

Recently SAUVAGEAU has discovered what he believes to be the gametophyte of *Phyllaria reniformis* in the tissues of *Lithophyllum lichenoides* (32). Finally, there has appeared a preliminary note by WILLIAMS (38) relating to a detailed study of cultures of *Laminaria* and *Chorda*, with descriptions of the gametophytes of these genera essentially as previously outlined. In addition, he mentions having observed the fusion of the gametes and even of the gamete nuclei of *Laminaria*, completing the morphological evidence of alternation of generations in that genus.

Classification

It now remains to be seen what effect these recent discoveries will have on our ideas of the grouping of the genera of the brown algae. The standard text on the brown algae to date is that of OLTMANNS (14), published in 1904–1905. The classification used there differs from that of KJELLMAN of 1891 (6) in several features, notably in the reinclusion of the Dictyotales in the Phaeophyceae with the Fucaceae, and in the reduction of several groups of the Phaeosporeae from the rank of families, including them under the Ectocarpaceae. The classification accepted by LOTSY (12) is nearly that of OLTMANNS. A recent table by SCHAFFNER (34) disregards all the more recent discoveries, giving four orders in the Phaeosporeae: Ectocarpales (isogamous), Laminariales (zoospores only), Cutleriales (anisogamous), and Tilopteridales (oogamous). In the Cyclosporeae he includes Fucales and Dictyotales. The obvious fact that only a small proportion of the genera known have been fully studied, and even that some families are only understood in the most fragmentary fashion, need not deter us from taking full advantage of the knowledge which is at hand. It must also be borne in mind in all cases that parthenogenesis and other kinds of short cuts in the life cycle may be present, and may be so characteristic of the ordinary propagation of the plant that the fundamental type of alternation upon which the classification is based may be obscured.

The orthodox division into two major groups, Phaeosporales and Cyclosporales, is still acceptable, provided the former is understood to include anisogamous as well as isogamous forms, and a widespread morphological alternation. The Cyclosporales include all oogamous groups, and may show a reduction from a morphological to a mere cytological alternation of generations. The first division of the Class PHAEOPHYCEAE is then the

Order PHAEOSPORALES.—This may be defined as having gametes isogamous to anisogamous. It includes three suborders, as follows:

Suborder ECTOCARPINEAE.—Morphological alternation of similar generations shown or inferred to be present.

Family 1. *Ectocarpaceae.*—Reproductive organs formed by the metamorphosis of all or part of a branch; growth of the free filaments intercalary. This is the primitive family of the class. In *Ectocarpus* the fusion of the elements from the plurilocular sporangia as gametes has been known since the work of BERTHOLD. Recently KYLIN (10) has reviewed the work on *Ectocarpus*, and contributed a study of two species, *E. siliculosus* and *E. tomentosus*. It is to be considered that the plants with sporangia (unilocular) and those with gametangia (plurilocular) normally alternate in the life cycle. Cases of abbreviation of this are well known, and peculiar conditions, as in *E. Padinae* Sauv., have been reported (33). The thallus is always primitively branching-filamentous, and intercalary growth is typical, but this becomes localized in some species into definite regions, while the hapteron branches and other attached or endophytic parts grow apically. These features are of importance as indicating the source of similar characters in the following families.

Family 2. *Tilopteridaceae.*—Reproductive elements of two kinds, small motile cells which may function as isogametes, and larger non-motile cells often with more than one nucleus. These latter cells are of two kinds according to some accounts, representing eggs without a membrane and but one nucleus, and monospores with a membrane and usually four nuclei. The oogamous character of this family has long been tentatively accepted, but has never been proved absolutely. On the basis of vegetative characters and an assumed isogamy, this family would stand in close relationship to the Ectocarpaceae, but if oogamy is actually present it would need to be placed in the Cyclosporales as a suborder Tilopteridineae preceding the Dictyotinieae, differentiated by the thallus characters and the incomplete division of the spores. For a discussion of literature see KYLIN (9).

Family 3. *Sphacelariaceae.*—Reproductive elements formed by the metamorphosis of all or part of a branch, growth from an apical cell. The originally monosiphonous filament usually divides up by internal walls, and may develop a peripheral meristematic zone producing a very considerable increase in thickness. Special vegetative methods of reproduction are present in most forms. SAUVAGEAU (20) reports finding egg and sperm production on one individual of *Halopetris scoparia*, but could only find one type of gametangium in *Cladostephus*. If this observation is confirmed, it will either force *Halopetris* into the Cyclosporales, a removal of the whole family from its present position, or necessitate a wider interpretation of the Phaeosporales. The family as understood here includes the Choristocarpaceae of KJELLMAN.

Family 4. *Asperococcaceae.*—Reproductive organs formed by the metamorphosis of, or as an outgrowth from, a superficial cell; growth intercalary. This family corresponds to the Encoeliaceae, Striariaceae, and Myriotrichaceae of KJELLMAN, the latter two representing simpler forms with the same essential construction. Plants are derived from a simple filament, becoming parenchymatous, either cylindrical or flattened. All stages can be traced. Gametangia with isogametes and sporangia are present, and considerable portions of the life history are known, especially of *Asperococcus* and *Scytosiphon* (10). The statement of YENDO (43) that the products of the plurilocular sporangia of *Phyllitis* are not gametes, but give rise to a microscopic gametophyte, requires confirmation.

Family 5. *Chordariaceae.*—Thallus differentiated into axial and assimilative filaments, branched, meristem localized; sporangia replacing assimilative filaments or modified segments therefrom. Essentially filamentous, the final short branches of the axial filaments turn outward and form a close cortex rich in chromatophores. Since both sporangia and gametangia are known in these genera, the life history is probably the same as that of *Ectocarpus*. The Elachisteaceae of KJELLMAN represent a reduced epiphytic group, and may best be included in the Chordariaceae.

Family 6. *Desmarestiaceae.*—Reproductive organs formed by the metamorphosis of, or as an outgrowth from, a free (or corticating) branch cell; growth trichothallic. The main axis in these forms is ramified, and produces short corticating branches, as well as (in some) delicate free ones. Little is known regarding the development of these genera; unilocular sporangia only are present, and there may be the same life history as in *Dictyosiphon*.

Family 7. *Stilophoraceae.*—Reproductive organs lateral on special branched supports, thallus erect on the substratum. As understood here, this family includes KJELLMAN's Stilophoraceae, Spermatochnaceae, and Sporochnaceae. The sporangia are borne on branched filaments developed from superficial cells of the thallus, and both sporangia and gametangia are known. Parts of the life cycle have been traced by KYLIN (10).

Family 8. *Ralfsiaceae.*—Reproductive organs at least in part lateral on special branched supports, thallus incrustating. Here we may include with the Ralfsiaceae also KJELLMAN's Lithodermataceae. In both the gametangia are borne laterally on special branched filaments arising from the surface, but the sporangia are only so borne in the Ralfsiaceae, in *Lithoderma* being but modified surface cells. The life history is unknown from the experimental viewpoint.

Suborder DICTYOSIPHONINEAE.—Morphological alternation of dissimilar generations present or inferred, the sporophyte exceeding the gametophyte in size.

Family *Dictyosiphonaceae.*—Characters of the suborder. The forms are branching, have an apical cell, and differentiate axial and cortical areas. The life history, worked out by SAUVAGEAU (31), has previously been described. This is a very important group, as it indicates an intermediate step in the development of a microscopic oogamous thallus, such as is shown in *Laminaria.*

Suborder CUTLERINEAE.—Morphological alternation of similar or of dissimilar generations present, gametophyte when different larger than the sporophyte; growth trichothallic.

Family *Cutleriaceae.*—Characters of the suborder. The life history of this group is well known, thanks to the cultural studies of SAUVAGEAU, CHURCH, and several others, and to the cytological studies of YAMANOUCHI on *Cutleria* (40, 41) and *Zanardinia* (42). The alternation shown by the cultural studies has been shown to be associated with a haploid and diploid nuclear constitution, reduction taking place in the sporangia. In *Zanardinia* the two generations are essentially alike, but in *Cutleria* the reduced and flattened sporophyte was long known as *Aglaozonia*, and thought to be an entirely different genus.

Order CYCLOSPORALES.—Plants of this order are strictly oogamous.

Suborder DICTYOTINEAE.—Morphological alternation of similar generations present.

Family *Dictyotaceae.*—Characters of the suborder. The gametangia are aggregated into definite areas or sori, and the asexual reproduction is by tetrasporangia, motile zoospores being replaced by four non-motile elements. The life cycle of *Dictyota* is fully known. Cultural studies showing the course of the development have been made by HOYT (3), and cytological studies by MOTTIER (13) and WILLIAMS (35, 36), showing reduction in tetraspore formation.

Suborder LAMINARINEAE.—Morphological alternation of dissimilar generations present, gametophyte smaller than the sporophyte.

Family *Laminariaceae.*—Characters of the suborder. Members of this family are almost all large plants. Reproduction was thought to be strictly by zoospores until SAUVAGEAU showed that the zoospores produced a microscopic gametophyte. The results of the various studies have previously been described.

Suborder FUCINEAE.—Only cytological alternation of generations present.

Family *Fucaceae.*—Characters of the suborder. This family forms the spores within pits or conceptacles. Still inclosed, the spores undergo a few cell divisions, or even only a few nuclear divisions, forming the gametes which are then shed as egg and sperm. Cytological studies have been made by several workers, including YAMANOUCHI (39), confirming the morphological and cultural observations. This is the climax family of the brown algae, and represents the greatest reduction of the gametophyte possible while still retaining an alternation.

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